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FIRE EFFECTS IN A MONTANE WETLAND, CENTRAL CASCADE RANGE, OREGON

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ABSTRACT

The stand-replacing Charlton, OR wildfire of 1996 burned several vegetation transects established before the fire, providing an opportunity to document recovery in one upland and five wetland vegetation zones over a 12-year period. Total mean percent cover of vegetation recovered to about 48% of pre-burn levels by year 12. Total cover increased slightly in *Carex* fen, but decreased in the other five zones. Fire damage was inversely proportional to moisture gradient, and recovery more or less directly proportional to the gradient. Upland *Tsuga mertensiana* forest sustained the greatest damage and showed the least recovery by year 12, followed by seasonally-flooded *Polytrichum commune* moss bed, *Xerophyllum tenax* ecotone, *Vaccinium uliginosum* shrub swamp, grass-dominated fen, and *Carex* fen. A transient soil crust of early-seral bryophytes occurred in upland *Tsuga mertensiana* forest. Cover of shrub, forb, grass, and moss layers declined in vegetation zones at the drier end of the moisture gradient, but increased in grass and sedge-dominated zones at the wetter end of the gradient, at the expense of forb, grass, and sedge layers.

Key Words: Cascade Range, fen, fire, peatland, vegetation, wetland.

Evidence of fire in wetlands of the Pacific Northwest is widespread, but few regional studies have examined the role of fire in these habitats. Hansen (1941, 1944) and Torgerson et al. (1949) reported charcoal and burned peat at depths of 1–2 m in organic soils along the coasts of Oregon and Washington. Martin and Frenkel (1978) and Kunze (1994) reported evidence of fire in fens along the coast and in the southern Puget Trough, and charred snags are present in peatlands at all elevations (Christy, unpublished data). Heinselman (1963) and others clearly demonstrated how fire can regulate vegetation succession in wetlands, but information about its effect in wetlands of the Pacific Northwest is sparse. Repeat photography and transect studies indicate that in the absence of fire, both cover and diversity of herbaceous peatland species decline with increasing competition from woody vegetation, as these habitats convert to shrub swamp and forested wetland (Schultz 1989; Guerrant et al. 1998; Hebda et al. 2000; Christy 2005a; Cramer 2005; Ratchford et al. 2005; Sanders et al. 2007; Tolman 2006, 2007).

Frenkel at al. (1986) described fen vegetation sampled in 1976 at the Torrey-Charlton Research Natural Area (RNA) in the central Cascade Range of Oregon. As part of the USDA Forest Service Pacific Northwest Region's RNA baseline monitoring program, ecologists resampled Frenkel's transect and established three others in 1993 to document ecotone conditions across wetlands. In 1996 the stand-replacing Charlton wildfire, part of the Moolack Fire Complex, burned 37.7 km^2 surrounding the study site (Fig. 1). The fire killed more than 95 percent of the forest over about three-quarters of the burn area (Gardner and Whitlock 2001; Acker et al. 2013), and many areas burned to mineral soil. Wetlands in the RNA sustained surface damage, but peat did not burn because it was wet enough to prevent ignition. After the fire, the four transects were reestablished and resampled periodically over the next 12 yr. Although fen vegetation in a number of other montane wetlands in Oregon has been documented in detail (Seyer 1979, 1981, 1983; Wilson 1986; Titus and Christy 1997; Christy and Titus 1998; Murray 2000; Christy 2001, 2003, 2005b, Greene

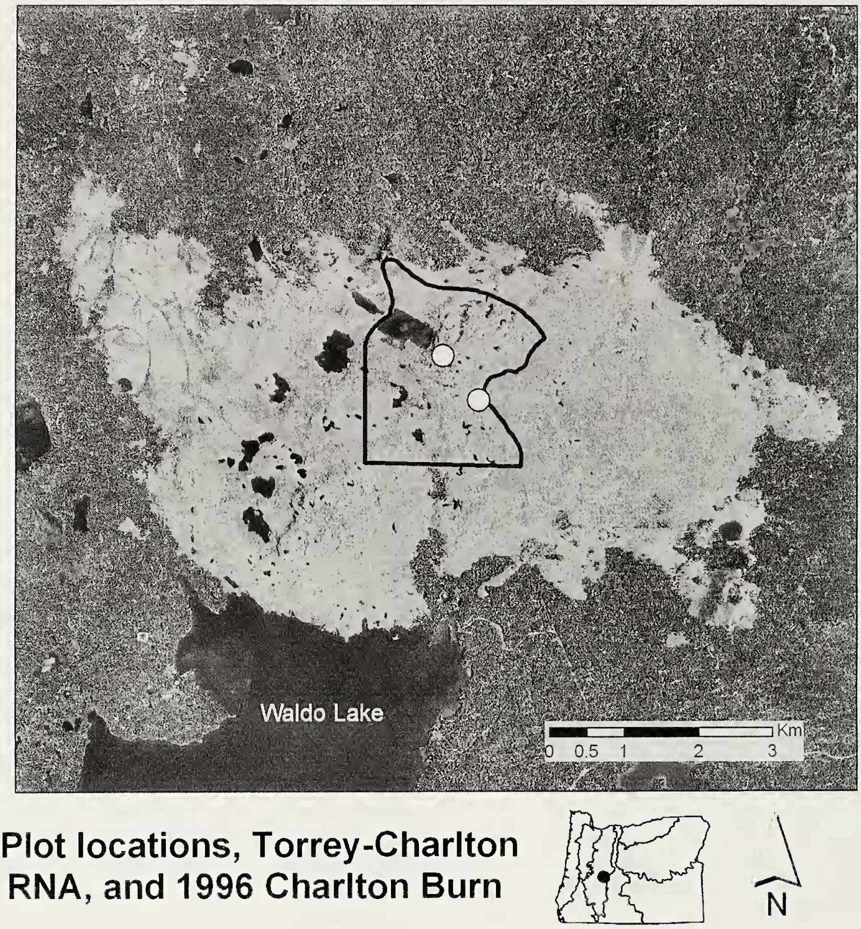

FIG. 1. Torrey Lake plots (white dots), Torrey-Charlton RNA boundary (black line), and extent of 1996 Charlton Burn (light-colored area).

and Schuller, unpublished data), none have pre- and post-burn data available.

Site-specific data on pre-disturbance vegetation, intensity of disturbance, and condition of survivors can facilitate interpretation and prediction of community response to disturbance (Attiwill 1994; Turner et al. 1997; Zobel and Antos 1997). In contrast to charcoal, pollen, and carbon storage analyses that document long-term changes wrought by fire and climate change, the study at Torrey-Charlton RNA provides scarce short-term pre- and post-burn data for a fen in the Pacific Northwest. Although a single-disturbance study has obvious limitations because of pseudo-replication (Turner et al. 1997), fire effects observed at the RNA will facilitate further studies in the region.

Study Site

Frenkel et al. (1986) described details of the study site, located at 43°47′46″N, 122°00′36″W. The Torrey-Charlton RNA was formally established by the USDA Forest Service in July 1998 (Salix Associates 1998), with the study area located in the Torrey Lake Unit of the RNA (Fig. 1). The site is located entirely within the Waldo Lake Wilderness Area, and is surrounded by other wilderness and roadless areas.

Hydrology

Snowpack, summer precipitation, and temperature varied over the 12-year sampling period, typical for montane wetlands in the Cascade Range. *Carex* fen, normally the wettest vegetation zone sampled at the site, exhibited varying amounts of bare ground, muck, or water in August and September, the driest part of the sampling years. Bare ground, muck, and water covered 58% of the plots in 1993, 96% in 1997, and 78% in 2001, consistent with precipitation recorded at Oakridge, Oregon, about 38 km WSW of the study area (Western Regional Climate Center 2010). During the sampling period, 1331 mm of precipitation were recorded at Oakridge in the 1992–1993 water year,

TABLE 1. SAMPLE SIZES, PER SAMPLING YEAR.

Vegetation zone	Sample year	Postfire year	Number transects	Number plots
Tsuga mertensiana forest	1993	preburn	4	67
Tsuga mertensiana forest	1997	1	4	67
Tsuga mertensiana forest	2001	5	3	45
Tsuga mertensiana forest	2008	12	2	34
Polytrichum commune moss bed	1993	preburn	1	6
Polytrichum commune moss bed	1997	1	1	6
Polytrichum commune moss bed	2001	5	1	6
Polytrichum commune moss bed	2008	12	1	6
Xerophyllum tenax ecotone	1993	preburn	3	16
Xerophyllum tenax ecotone	1997	1	3	16
Xerophyllum tenax ecotone	2001	5	3	16
Xerophyllum tenax ecotone	2008	12	1	13
Vaccinium uliginosum shrub swamp	1993	preburn	3	31
Vaccinium uliginosum shrub swamp	1997	1	3	31
Vaccinium uliginosum shrub swamp	2001	5	3	31
Vaccinium uliginosum shrub swamp	2008	12	1	11
Grass-dominated fen	1993	preburn	3	6
Grass-dominated fen	1997	1	3	6
Grass-dominated fen	2001	5	2	4
Grass-dominated fen	2008	12	1	2
Carex fen	1993	preburn	4	45
Carex fen	1997	1	4	45
Carex fen	2001	5	4	45
Carex fen	2008	12	2	26

1623 mm in 1996–1997, 777 mm in 2000–2001, and 1196 mm in 2007–2008.

METHODS

Sampling. The original 1976 transect of Frenkel et al. (1986) at Torrey Lake Fen was reestablished by Frenkel and USDA Forest Service ecologists in 1993. This transect and three others established nearby were sampled that same year following USDA Forest Service regional RNA ecotone transect protocols (USFS, unpublished), which differed slightly from those used by Frenkel et al. (1986). All transects were oriented perpendicular to wetland gradients, spanned the widths of the subject wetlands, and each endpoint was located in upland *Tsuga mertensiana* (Bong.) Carrière forest. Species cover was observed in 20 × 50 cm microplots, and recorded in absolute percent cover. Microplots along Frenkel's original transect matched locations of the originals at 0.5 and 1 m intervals, and the transects established in 1993 were sampled at 1 m intervals. Mature trees were tagged in a belt 5–10 m wide along each transect, recording species and dbh, but percent canopy cover was not recorded. For this variable we used the plot-based estimate from Frenkel et al. (1986), which approximated conditions in all four transects in 1993. Because the reestablished transect may not have replicated the exact location of the original, we used the data from 1993 as our pre-burn benchmark. Community composition and zonation observed in 1993 remained essentially unchanged from Frenkel's original descriptions. All transects were resampled periodically over the next 12 yr, but not all transects were resampled in a given year because of budget and time constraints (Table 1).

Data analysis. We sorted plots from all transects into six vegetation zones that had been demarcated at the time of pre-burn sampling in 1993 (Table 2), and then summarized plot data as means per zone, per sample year. We used the same *Tsuga mertensiana* and *Xerophyllum tenax* (Pursh) Nutt. zone concepts of Frenkel et al. (1986), but to simplify interpretation of fire response we combined their two sedge types and two wet shrub types to one of each.

Per vegetation zone and sample year, we summarized (1) percent cover and frequency of dominant species, (2) total vascular plant cover, and (3) total cover per vegetation layer. We omitted species with mean cover of less than 10 percent for all sample years from analysis of dominant species response, but included them in analysis of total vascular plant cover, and cover per vegetation layer. We omitted percent cover of abiotic features (litter, bare ground, fire evidence, etc.) in data analysis, but included observations of same in qualitative descriptions of fire effects. Values indicating recovery from fire represent both positive and negative percent change between 1993 and the most recent sample year, added to 100.

TABLE 2. CROSSWALK OF VEGETATION ZONES USED HERE AND BY FRENKEL ET AL. (1986).

Current study	Frenkel et al. (1986)
Tsuga mertensiana forest	*Tsuga mertensiana / Vaccinium scoparium* Forest
Polytrichum commune moss bed	Not present in transect of Frenkel et al.
Xerophyllum tenax ecotone	Xerophyllum tenax Fringe
Vaccinium uliginosum shrub-swamp	*Kalmia microphylla / Sphagnum* Bog, *Vaccinium occidentale / Trifolium longipes* Thicket
Grass-dominated fen	Not present in transect of Frenkel et al.
Carex fen	*Carex rostrata* Reedswamp, *Carex sitchensis* Fen

The sampling period spanned 12 yr. We selected data from 1993, 1997, 2001, and 2008 because they were the most complete, with two exceptions: (1) data for grass-dominated fen from 2008 were excluded because only two plots were sampled, and (2) the *Polytrichum commune* Hedw. moss bed was not sampled in 2001, so we used data from 2005 instead.

Botanical nomenclature. Botanical nomenclature follows the Oregon Flora Project's Oregon Vascular Plant Checklist (Cook et al. 2013). Names of plant associations follow McCain and Diaz (2002) and Christy (2004).

RESULTS

For the six vegetation zones over the 12-year sampling period, mean percent cover and frequency of dominant species are shown in Table 3. Mean and total percent cover for each vegetation layer and vegetation zone, the percent change between pre-burn and most recent sample year, and rate of recovery are shown in Figure 2 and Table 4. For convenience, vegetation zones are ordered in this paper along a hydrological gradient from driest to wettest.

Tsuga mertensiana forest (Figs. 3, 9, 10; Tables 3 and 4). Before the fire, wetlands at the study site were surrounded by upland forest of old-growth *Tsuga mertensiana* with a canopy cover of about 80% (Frenkel et al. 1986). Cores taken in 1993 from trees around the edge of the fen indicated that the forest originated from a stand-replacing fire that occurred between 1700 and 1750 (*Tsuga mertensiana* 8–63 cm dbh, 91–290 yr old, *Pinus monticola* Douglas ex D. Don 46 cm dbh, 250 yr old, *Pinus contorta* var. *latifolia* Engelm. 8–30 cm dbh, 70–234 yr old). Slow growth and small diameters are typical of this forest type. Of all vegetation zones sampled, fire effects were most severe in *Tsuga mertensiana* forest, and recovery of total cover was the slowest of any zone, reaching about 19% of pre-burn levels by year 12. All trees were killed by flame heights of up to 15 m, and 55–98% of duff and organic material were consumed, except near the edge of the wetland where loss was 0–50%. Burned snags remained abundant in the RNA ten years after the fire (Acker et al. 2013). Density of tree seedlings in severely burned plots, dominated by *Pinus contorta* var. *latifolia* that was extremely sparse even before the fire, was only 4% of that in unburned plots by year six. Most shrubs were killed and had not re-established by year two, and by year 12 total shrub recovery was only 21% of pre-burn levels. *Vaccinium scoparium* Leiberg ex Coville had trace amounts resprouting by year one, but only 2–3% cover by year five. Within 2 m of the wetland margin, *V. scoparium* and *V. deliciosum* Piper resprouted by year two but did not approach pre-burn abundance until year seven. After an initial drop, cover of forbs, grasses, and sedges increased slightly by year 12. At year one the native post-disturbance forb *Chamerion angustifolium* var. *canescens* (Alph. Wood) N. H. Holmgren & P. K. Holmgren established on some transects with very low cover in up to 25% of microplots, and increased to 2–3% by year two. After a slight drop of 1% from pre-burn cover, the moss layer increased to almost 9% by year 12. The liverwort *Marchantia polymorpha* L. (*sensu lato*) was widespread and conspicuous on burned soil in intermittent streambeds and small depressions in years one and two, but by year three it was replaced by the moss *Ceratodon purpureus* (Hedw.) Brid. with localized cover of 5–30%, and by year seven the moss *Polytrichum juniperinum* Hedw. was conspicuous. Fire effects continued to impact this zone after year 12 as accelerating decay of dead trees contributed increasing amounts of coarse wood.

Polytrichum commune moss bed (Figs. 4, 11; Tables 3 and 4). Before the fire, extensive monotypic beds of *Polytrichum commune* occurred in shallow, seasonally-flooded glacial potholes (Christy 2004). This vegetation zone was located just below the fringing upland *Tsuga mertensiana* forest, and had a total mean percent cover of 83%. The fire scorched or killed 60–99% of *Polytrichum* mats in the single transect sampled, and similar effects were observed in nearby potholes. Some stands exhibited only 1% cover at year one, but increased to 10% at year two, regenerating from uninjured tissue within thicker, moist mats. *Polytrichum* recovered to some extent by year nine, but by year 12 it had declined to only 21% of pre-burn levels. Graminoids (*Carex exsiccata*,

TABLE 3. MEAN PERCENT COVER AND FREQUENCY OF DOMINANT SPECIES, BY VEGETATION ZONE AND SAMPLE YEAR. Estimate of canopy cover for *Tsuga mertensiana* forest from Frenkel et al. (1986).

Vegetation zone	Dominant Species	1993 Mean	1993 Freq	1997 Mean	1997 Freq	2001 Mean	2001 Freq	2008 Mean	2008 Freq
Tsuga mertensiana forest									
	Tsuga mertensiana	80.00	100.00	0.00	0.00	0.00	0.00	0.00	0.00
	Vaccinium scoparium	17.00	12.30	0.04	2.00	2.70	3.00	3.67	4.00
	Xerophyllum tenax	5.70	3.00	1.00	1.30	3.40	1.30	8.67	3.00
	Moss	1.40	13.00	1.00	3.00	11.00	11.70	6.58	5.00
Polytrichum commune moss bed ("2001" = 2005)									
	Calamagrostis canadensis	0.00	0.00	0.00	0.00	0.00	14.29	1.14	42.86
	Carex exsiccata	0.14	14.29	0.00	0.00	9.43	42.86	12.73	71.43
	Deschampsia cespitosa	0.00	0.00	0.01	14.29	21.43	42.86	5.00	71.43
	Polytrichum commune	72.86	100.00	3.74	100.00	21.43	57.14	15.00	57.14
Xerophyllum tenax ecotone									
	Xerophyllum tenax	60.30	5.30	27.00	5.00	42.70	4.30	48.38	13.00
	Vaccinium scoparium	17.50	1.00	0.03	0.30	5.00	0.70	0.00	0.00
	Gaultheria humifusa	0.00	0.00	0.00	0.00	5.80	0.30	0.00	0.00
	Sphagnum sp.	19.70	2.00	0.70	0.30	0.80	0.70	0.31	2.00
	Moss	4.00	3.30	0.20	1.00	4.30	1.30	2.00	9.00
Vaccinium uliginosum shrub swamp									
	Vaccinium uliginosum	21.40	10.30	11.40	7.70	11.10	5.70	18.00	12.00
	Kalmia microphylla	5.90	9.00	1.90	6.30	4.10	6.70	2.36	7.00
	Vaccinium deliciosum	2.50	1.70	0.10	0.60	4.40	1.70	1.29	2.00
	Xerophyllum tenax	1.30	1.00	6.70	0.70	9.60	1.00	0.00	0.00
	Podagrostis thurberiana	3.70	2.60	0.20	1.00	0.00	0.00	0.00	0.00
	Sphagnum sp.	42.30	8.30	26.50	6.00	29.30	4.70	15.00	8.00
	Moss	13.40	8.70	4.20	2.70	10.20	6.00	10.72	12.00
Grass-dominated fen									
	Calamagrostis canadensis	22.80	1.30	5.00	0.60	2.50	1.50	n/a	n/a
	Deschampsia cespitosa	15.80	0.70	4.20	0.70	0.00	0.00	n/a	n/a
	Sphagnum sp.	30.00	0.70	25.00	0.70	60.00	1.00	n/a	n/a
	Vaccinium uliginosum	3.30	1.00	1.30	0.70	7.30	1.00	n/a	n/a
	Carex exsiccata	1.00	1.30	12.70	1.30	4.50	1.00	n/a	n/a
	Moss	9.80	1.00	0.00	0.00	0.00	0.00	n/a	n/a
Carex fen									
	Carex aquatilis var. *dives*	6.80	7.00	2.50	5.00	4.25	3.00	2.50	4.50
	Carex buxbaumii	4.30	4.50	1.50	3.30	6.30	1.80	3.60	5.50
	Carex exsiccata	25.60	10.30	5.00	7.00	4.70	3.50	5.90	7.00
	Deschampsia cespitosa	3.60	3.50	1.00	1.50	0.10	0.30	0.90	1.50
	Sphagnum sp.	2.50	3.80	2.40	1.80	5.20	3.30	10.70	8.00
	Moss	3.40	6.00	0.40	1.00	2.70	3.30	0.10	1.00

Eleocharis acicularis [L.] Roem. & Schult., *Glyceria* R. Br., *Calamagrostis canadensis* [Michx.] P. Beauv.) appeared where none had existed before the burn, with mean covers of 7% and 8%, respectively.

Xerophyllum tenax ecotone (Figs. 5, 9, 10; Tables 3 and 4). Before the fire, another upland-wetland ecotone was characterized by a 3–5 m wide band of the forb *Xerophyllum tenax* and shrubs that occurred around margins of wetlands (Frenkel et al. 1986). *Xerophyllum tenax* was the dominant species with a mean cover of 60%. This zone was severely burned by the fire, and much of the vegetation at the drier upland edge was killed. Total cover in year 12 reached 64% of pre-burn levels, the third slowest of the zones sampled. All growth forms except graminoids exhibited reduced cover. Pre-burn covers of up to 80% *Xerophyllum* in some transects were reduced to 15% in year one and 40% in year two. Browned or charred *Xerophyllum* at the wetter end of the zone resprouted 14 d after the fire, and some stands recovered fully by year one. By year 12, shrub recovery was only 42% of pre-burn levels. *Rubus lasiococcus* A. Gray and *Vaccinium membranaceum* Douglas ex Torr. at the wetter end of the zone recovered to near pre-burn levels by year two. *Gaultheria humifusa* (Graham) Rydb., *Kalmia microphylla* [Hook.] A. Heller, *Spiraea*

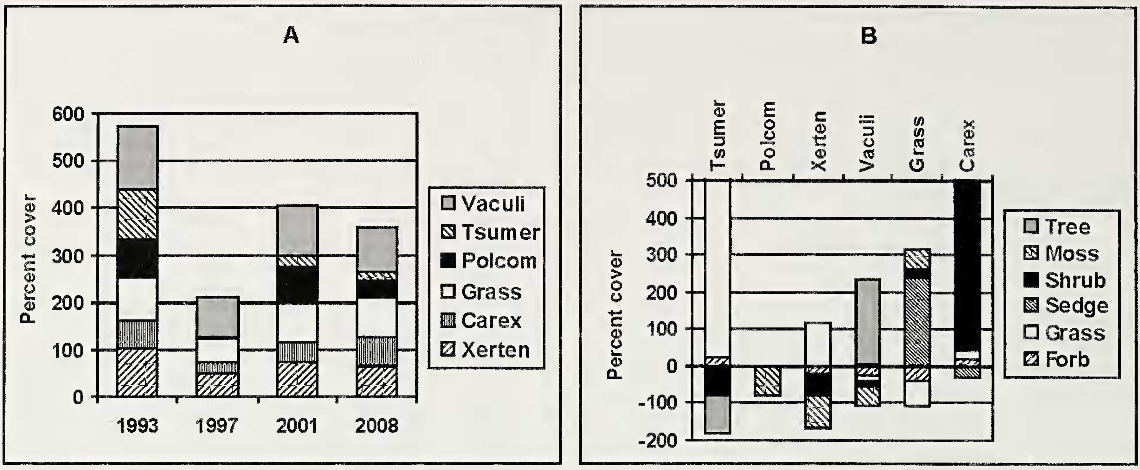

FIG. 2. Overall fire response, 1993–2008. A. Mean total percent cover by vegetation zone and sample year. B. Change in mean total percent cover by vegetation layer, vegetation zone, and sample year. Carex—*Carex* fen; Grass—Grass-dominated fen; Polcom—*Polytrichum commune* moss bed; Tsumer—*Tsuga mertensiana* forest; Vaculi—*Vaccinium uliginosum* shrub swamp; Xerten—*Xerophyllum tenax* ecotone.

splendens Baumann ex K. Koch, *Vaccinium deliciosum, V. scoparium* and *V. uliginosum* L. died or had trace resprouting by year one, and only 5% cover by year five. Grasses showed a slight increase in cover, and sedges appeared where none had existed in 1993, but cover of both was less than 2%. The moss layer was killed by the fire, and recovery to only 13% of pre-burn levels by year 12 was the poorest for any layer in any of the vegetation zones.

Vaccinium uliginosum shrub swamp (Figs. 6, 9, 10; Tables 3 and 4). Before the fire, *Vaccinium uliginosum* shrub swamp (= *Vaccinium occidentale* A. Gray and *Kalmia microphylla* [Hook.] A. Heller communities of Frenkel et al. 1986) had the highest mean total cover of shrubs (35%) of any zones sampled, with *Sphagnum* L. covering more than 40% of the moss layer. Total percent cover of vascular plants recovered to 92% of pre-burn levels by year 12, but all growth forms except tree and sedge exhibited diminished cover. Overall, shrubs recovered 84% by 2008. Many were top-killed immediately after the fire but resprouted by year one, except for *Vaccinium scoparium* that was not detected until year five. *Vaccinium deliciosum* was inconspicuous until year four. *Vaccinium uliginosum* recovered to 84% of pre-burn levels by year 12, but *Kalmia microphylla* and *Vaccinium deliciosum* had recovered to only 41% and 52%, respectively. Tree islands within *Vaccinium uliginosum* shrub swamp were far enough away from the upland that they did not burn, and these contained the only surviving trees along the transects. Total forb and grass recovery by 2008 were 76% and 86%, respectively. *Chamerion angustifolium* established in shrub swamp by year one but had nearly disappeared by year two. Sedge showed a 106% increase, but total cover was less than 9%. In contrast to vascular plants, the moss layer had the lowest (47%) recovery of any layer in this zone, and the third poorest overall recovery after the *Xerophyllum tenax* ecotone and *Polytrichum commune* moss bed. *Aulacomnium palustre* and *Polytrichum commune* had returned to 80% of pre-burn levels by year 12, but the once-dominant *Sphagnum capillifolium* had recovered only 36% of its former abundance.

Grass-dominated fen (Fig. 7; Tables 3 and 4). Before the fire, grass-dominated fen occurred as patches of *Calamagrostis canadensis* and *Deschampsia cespitosa* within a matrix of *Vaccinium uliginosum* shrub swamp and *Carex* fen. The moss layer had a mean cover of 40%, dominated by lawns of *Sphagnum capillifolium* with a mean cover of 30% and absolute cover in individual stands up to 90%. Photos taken immediately after the fire showed that *Calamagrostis canadensis, Deschampsia cespitosa, Kalmia microphylla, Spiraea splendens*, and *Vaccinium uliginosum* were badly burned. Total mean percent cover of vascular plants recovered to 50% of pre-burn levels by year five, with forb and grass layers recovering 63% and 28%, respectively. In contrast, the shrub, sedge, and moss layers increased total mean cover by 24% (to 7% cover), 238% (to 5% cover), and 51% (to 60% cover), respectively, over pre-burn levels.

Carex fen (Figs. 8, 9, 10; Tables 3 and 4). Before the fire, *Carex* fen (= *Carex rostrata* Reedswamp and *Carex sitchensis* Fen of Frenkel et al. 1986) was a mix of *Carex aquatilis* var. *dives, Carex buxbaumii*, and *Carex exsiccata* occurring in seasonally to perennially flooded

TABLE 4. MEAN AND TOTAL PERCENT COVER BY VEGETATION LAYER, VEGETATION ZONE, AND SAMPLE YEAR. Estimate of canopy cover for *Tsuga mertensiana* forest from Frenkel et al. (1986). Percent change calculated using preburn (1993) and most recent sample year available per vegetation zone.

Vegetation zone	Vegetation layer	Sample year				Percent change	Recovery
		1993	1997	2001	2008		
Tsuga mertensiana forest							
	Tree	80.00	0.00	0.00	0.00	−100.00	0.00
	Shrub	19.37	0.09	4.16	4.09	−78.89	21.11
	Forb	4.13	0.96	6.18	5.01	21.31	121.31
	Grass	0.07	0.18	1.11	1.91	2628.57	2728.57
	Sedge	0.07	0.00	0.44	0.12	71.43	171.43
	Moss	1.13	0.82	10.22	8.56	657.52	757.52
	TOTAL	104.77	2.05	22.11	19.69	−81.21	18.79
Polytrichum commune moss bed ("2001" = 2005)							
	Grass	0.00	0.02	25.00	6.50	n/a	n/a
	Sedge	0.00	0.00	1.00	8.37	n/a	n/a
	Moss	82.50	3.03	51.33	17.50	−78.79	21.21
	TOTAL	82.50	3.05	77.33	32.37	−60.76	39.24
Xerophyllum tenax ecotone							
	Shrub	16.88	1.84	9.19	7.10	−57.94	42.06
	Forb	67.38	45.6	57.33	54.17	−19.61	80.39
	Grass	0.75	0.13	1.06	1.62	116.00	216.00
	Sedge	0.00	0.00	1.25	1.15	n/a	n/a
	Moss	18.19	0.38	3.76	2.33	−87.19	12.81
	TOTAL	103.2	47.95	72.59	66.37	−35.69	64.31
Vaccinium uliginosum shrub-swamp							
	Tree	2.03	0.00	2.75	6.67	228.58	328.58
	Shrub	34.94	18.88	24.91	29.51	−15.54	84.46
	Forb	16.35	12.21	14.64	12.35	−24.46	75.54
	Grass	11.13	4.75	11.23	9.59	−13.84	86.16
	Sedge	8.19	3.41	9.78	8.67	5.86	105.86
	Moss	63.47	41.88	44.53	29.59	−53.38	46.62
	TOTAL	136.11	81.13	107.84	96.38	−29.19	70.81
Grass-dominated fen							
	Shrub	5.83	1.33	7.25	n/a	24.36	124.36
	Forb	2.00	0.33	1.25	n/a	−37.50	62.50
	Grass	39.50	9.17	11.25	n/a	−71.52	28.48
	Sedge	1.33	12.67	4.50	n/a	238.35	338.35
	Moss	39.83	25.00	60.00	n/a	50.64	150.64
	TOTAL	88.49	48.5	84.25	n/a	−4.79	95.21
Carex fen							
	Shrub	0.05	0.02	0.18	0.93	1760	1860.00
	Forb	8.24	8.92	3.55	9.93	20.51	120.51
	Grass	3.63	1.55	0.33	4.41	21.49	121.49
	Sedge	40.92	11.59	23.72	29.42	−28.10	71.90
	Moss	5.96	3.57	13.53	15.22	155.37	255.37
	TOTAL	58.80	25.65	41.31	59.91	1.89	101.89
TOTAL All Vegetation Zones							
		573.87	208.33	405.43	358.97	−52.13	47.87

depressions. It is the wettest of all zones sampled. Photos taken immediately after the burn showed that *Carex* fen did not carry a fire and showed no obvious fire effects, and the moss layer charred or burned only where brands landed on it, or where preexisting logs burned into the fen. By year 12, total mean percent cover recovered to 102% of pre-burn levels. Sedges recovered to only 72% of pre-burn levels, and total mean cover increased very slightly for shrubs and grass (less than 1%), forbs (1%), and moss (9%). After a decline immediately following the fire, mean cover of *Sphagnum* increased 166% by year 12.

DISCUSSION

By year 12, overall recovery of all six vegetation zones had reached only about 48%

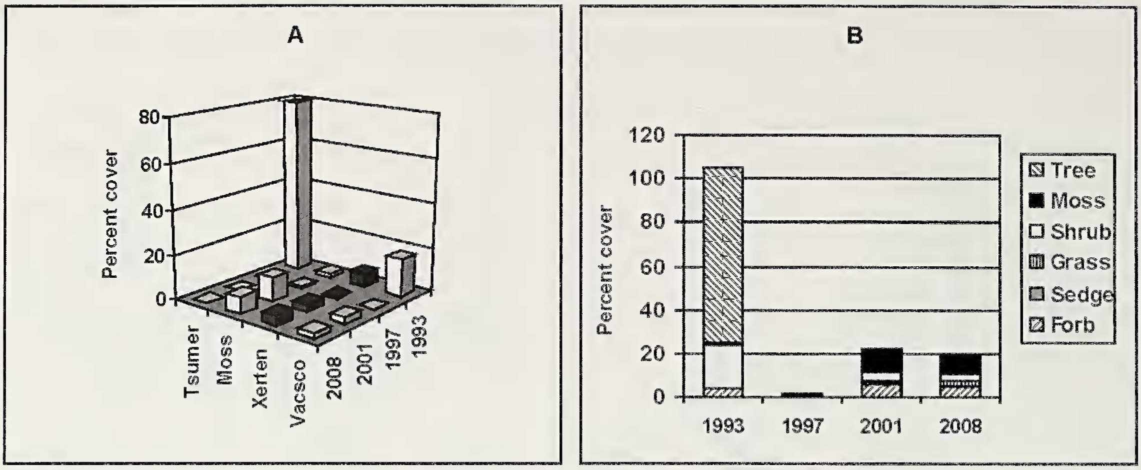

FIG. 3. Fire response in *Tsuga mertensiana* forest, in mean percent cover. A. Dominant species. B. Vegetation layers. Tsumer—*Tsuga mertensiana*; Vacsco—*Vaccinium scoparium*; Xerten—*Xerophyllum tenax*. Figures do not include canopy cover of mature trees (see text). Obscured in 3A: Tsumer 1997 = 0.

of the pre-burn baseline, and persistent reduced cover in some layers indicated that fire effects were still evident 12 yr after the event (Figs. 2, 9, 10; Table 4). Field observation of the six vegetation zones immediately after the fire indicated that the upland *Tsuga mertensiana* forest had sustained the most severe fire damage, followed in diminishing order by *Polytrichum commune* moss bed, grass-dominated fen, *Xerophyllum tenax* ecotone, *Vaccinium uliginosum* shrub swamp, and *Carex* fen. However, recovery did not parallel the immediate post-fire impacts observed in 1996.

Upland Response. The fire was a catastrophic event for upland *Tsuga mertensiana* forest, killing all trees and most of the shrubs (Figs. 2, 10, 11). The 250–300 yr fire return interval observed in the RNA was intermediate for reports of 100–460 yr (Dickman 1984; Dickman and Cook 1989; Gardner and Whitlock 2001). After an initial influx of *Pinus contorta* var. *latifolia*, recruitment of additional species at Torrey Lake Fen will be very slow (Acker et al. 2013). Burned forests of *Tsuga mertensiana* on the Olympic Peninsula of Washington took 55–88 yr to reestablish densities of fewer than 600 trees per hectare (Agee and Smith 1984).

Impacts from stand-replacing fire on forest trees and shrubs have been relatively well documented in the Pacific Northwest, and effects in the RNA (Table 5) generally followed patterns reported elsewhere. High mortality and slow recovery of *Gaultheria humifusa, Vaccinium deli-*

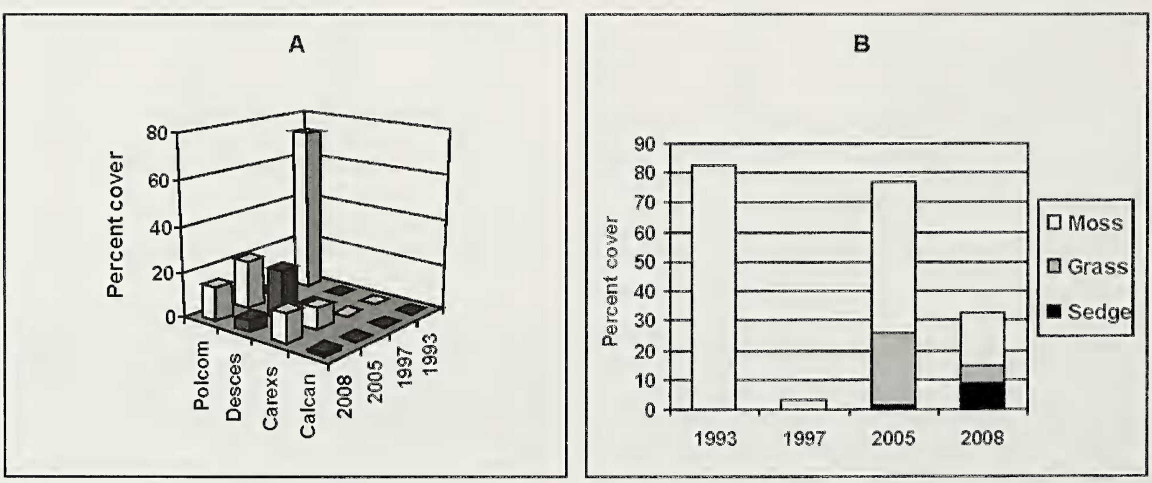

FIG. 4. Fire response in *Polytrichum commune* moss bed, in mean percent cover. A. Dominant species. B. Vegetation layers. Calcan—*Calamagrostis canadensis*; Carexs—*Carex exsiccata*; Desces—*Deschampsia cespitosa*; Polcom—*Polytrichum commune*. Obscured in 4A: Desces 1997 = 0, Polcom 1997 = 3.74.

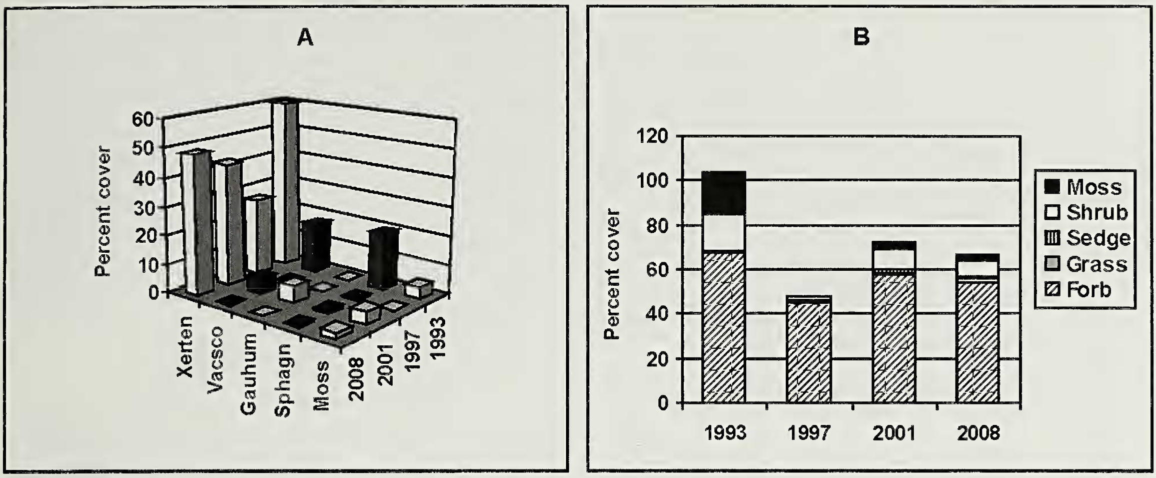

FIG. 5. Fire response in *Xerophyllum tenax* ecotone, in mean percent cover. A. Dominant species. B. Vegetation layers. Gauhum—*Gaultheria humifusa*; Sphagn—*Sphagnum* spp.; Vacsco—*Vaccinium scoparium*; Xerten—*Xerophyllum tenax*. Obscured in 5A: Vacsco 1997 = 0.03.

ciosum, and *Vaccinium scoparium* were similar to those reported by Matlack et al. (1993); Turner et al. (1997); Zobel and Antos (1997); and Hill and Vander Kloet (2005). Shallow-rooted species are more vulnerable to hot fires than deeper-rooted species, and soil moisture at the time of the burn is critical in determining shrub survival. The seed bank is often consumed in hot fires and recruitment is mediated by distance from surviving seed sources. In stand-replacing situations, resprouting therefore remains the only viable means for short-term recovery of understory species.

Despite the fact that fire effects were most severe in the *Tsuga mertensiana* forest, the amount of change in the understory was relatively small (Fig. 2b) because the shady pre-burn understory was never abundant. Increases in forbs, grasses, sedges, and moss over pre-burn levels can be attributed to release from canopy shading. In addition, the surge in bryophyte cover can be attributed to the flush of post-burn "fire mosses" mediated by pH and nutrients from ash. The appearance of a post-fire soil crust dominated by bryophytes has not been reported from the Cascade Range, and differs from the composition of pioneer species on newly-exposed soils (e.g., Zobel and Antos 1997). Transition from an initial bloom of the liverwort *Marchantia polymorpha* (*sensu lato*) in years one and two to the mosses *Ceratodon purpureus* by year three and *Polytrichum juniperinum* by year seven (Fig. 12) is

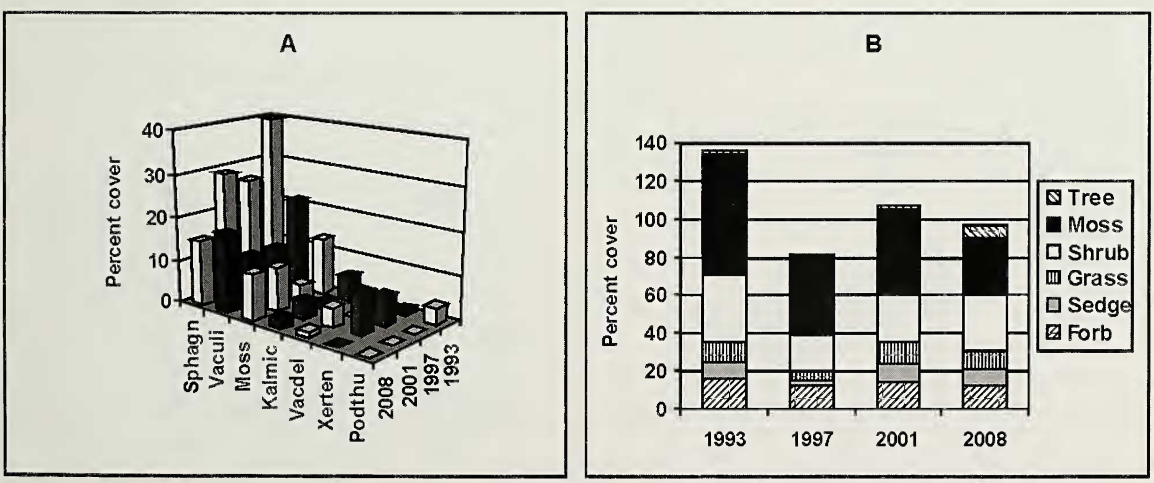

FIG. 6. Fire response in *Vaccinium uliginosum* shrub swamp, in mean percent cover. A. Dominant species. B. Vegetation layers. Kalmic—*Kalmia microphylla*; Podthu—*Podagrostis thurburiana*; Sphagn—*Sphagnum* spp.; Vacdel—*Vaccinium deliciosum*; Vaculi—*Vaccinium uliginosum*; Xerten—*Xerophyllum tenax*. Obscured in 6A: Kalmic 1997 = 1.9, Vacdel 1993 = 2.5, Vacdel 1997 = 0.1.

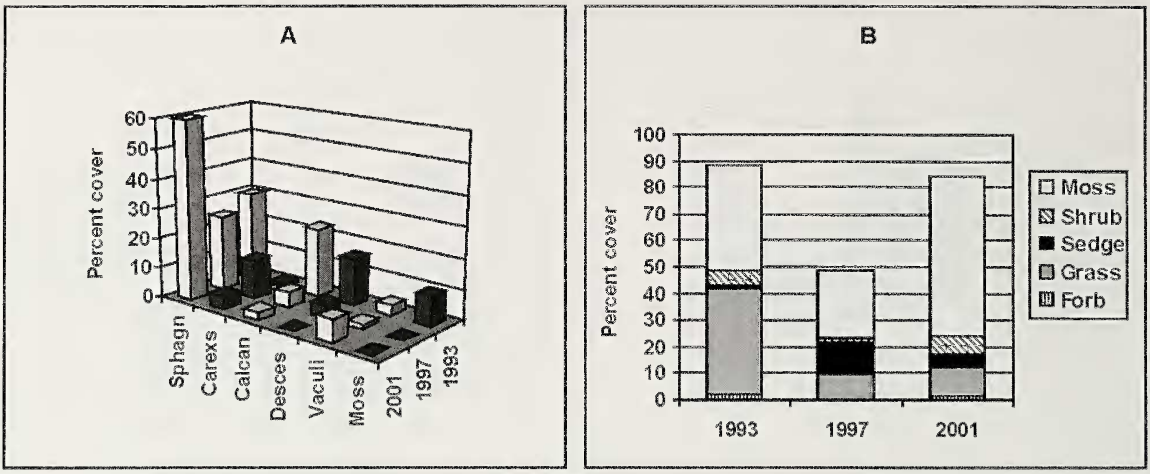

FIG. 7. Fire response in grass-dominated fen, in mean percent cover. A. Dominant species. B. Vegetation layers. Calcan—*Calamagrostis canadensis*; Carexs—*Carex exsiccata*; Desces—*Deschampsia cespitosa*; Sphagn—*Sphagnum* spp.; Vaculi—*Vaccinium uliginosum*.

similar to sequences observed elsewhere (Cremer and Mount 1965; DeBenedetti and Parsons 1984; Maltby et al. 1990; Tesky 1992; Matthews 1993; Thomas et al. 1994; Fryer 2008). Crusts formed by these species presumably play a role in ecosystem recovery similar to biological soil crusts reported from arid environments (e.g., Belknap et al. 2001; Ponzetti et al. 2007) by stabilizing soil, fixing atmospheric nitrogen, and creating seedbeds for invading vascular plants. In burned forests and peatlands, recovering vascular vegetation eventually shades out soil crusts, and their component species become much less common. Maltby et al. (1990) observed a decline in crusts between years six and 10, similar to what happened at the RNA.

Wetland Response. Frenkel et al. (1986) documented the extent of upland tree cover and shading around the edge of wetlands in the RNA. Removal of forest cover influences adjacent wetlands by increasing snowpack, soil moisture, runoff, streamflow, turbidity, light, and temperature (Moore and Bellamy 1974; Tiedemann et al. 1979; Pyne et al. 1996). Changes in nutrient status from runoff can boost productivity in wetlands, causing relatively short-lived changes in species composition. Pyne et al. (1996) estimated that hydrology and water quality can recover to pre-burn conditions within 5–10 yr. Recovery of wetland vegetation has been estimated to occur within 10–30 yr (Rowe and Scotter 1973; Tallis 1983; DeBenedetti and Parsons 1984; Kuhry

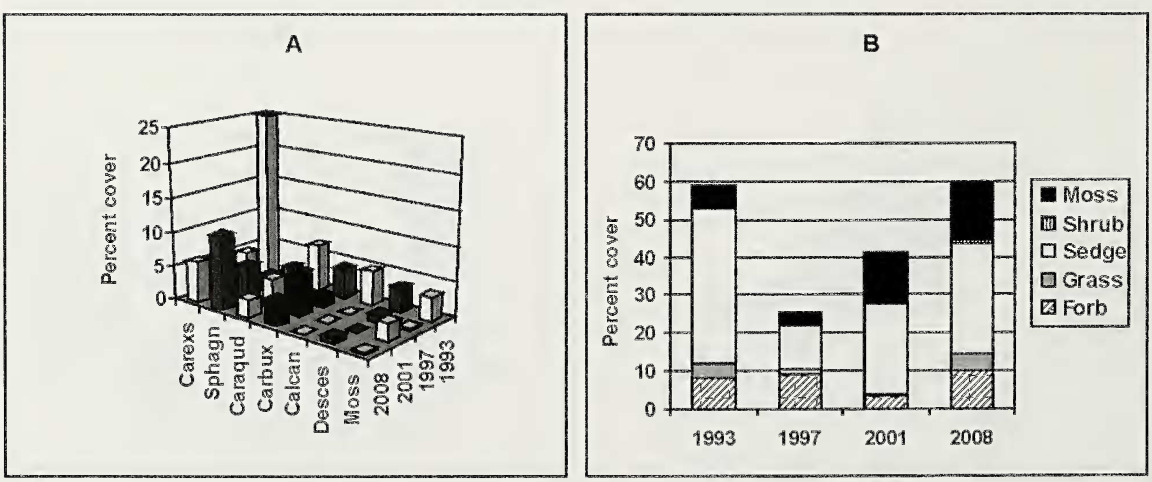

FIG. 8. Fire response *Carex* fen, in mean percent cover. A. Dominant species. B. Vegetation layers. Calcan—*Calamagrostis canadensis*; Caraqd—*Carex aquatilis* var. *dives*; Carbux—*Carex buxbaumii*; Carexs—*Carex exsiccata*; Desces—*Deschampsia cespitosa*; Sphagn—*Sphagnum* spp; Obscured in 8A: Carexs 2001 = 4.7, Sphagn 1993 = 2.5, Sphagn 1997 = 2.4.

FIG. 9. Original 1976 transect, view to north. A. 1981, before fire. B. 2011, 15 years after fire. Scale intervals in A = 10 cm. Transect length = 55 m.

1994; Ratchford et al. 2005; Kuhry and Turunen 2006).

As expected, fire effects at Torrey Lake Fen diminished with increasing soil moisture and distance from burned upland, but effects persisted even in the wettest zones. *Polytrichum commune* moss bed, *Xerophyllum tenax* ecotone, *Vaccinium uliginosum* shrub swamp, and grass-dominated fen burned more severely than *Carex* fen. *Vaccinium uliginosum* shrub swamp and *Carex* fen exhibited few immediate post-fire impacts at an average of 26 m (range = 16 to 31 m) from the perimeter of the burn, but 12 yr after the fire percent cover had not recovered to pre-burn levels, indicating that fire effects were more pervasive than initially apparent. Almost all vegetation layers showed reduced percent cover in *Polytrichum commune* moss bed, *Xerophyllum tenax* ecotone, *Vaccinium uliginosum* shrub swamp by year 12 (Table 4). In contrast, grass-dominated fen showed increases in shrub, sedge and moss layers, but decreases in forb (38%) and grass (72%) layers, while *Carex* fen showed increases in all layers except sedge, which declined 28%. These responses may be attributable in part to normal patch dynamics of rhizomatous populations as detected with repeat photography in other fens (e.g., Christy and Titus 1998).

The *Polytrichum commune* moss bed exhibited the second-greatest change in vegetation and had the second-poorest overall recovery rate by year 12. Survival of *Polytrichum* was mediated by moisture content in the moss bed and underlying soil at the time of the fire. Maltby et al. (1990) regarded beds of *Polytrichum commune* as a long-lived, fire-initiated system that eventually converts to vascular plants. However, in the Cascade Range, beds of *Polytrichum commune* persist in depressional wetlands as an integral component of old-growth *Tsuga mertensiana* forest (Christy, unpublished data). In the study area, their destruction was the only known wetland community where fire reset vegetation to a completely different seral stage dominated by graminoids (Fig. 11).

Recruitment and Recolonization. Survival of upland species around the edge of wetlands may be critical for recovery of upland communities. Compared to the upland *Tsuga mertensiana* forest, wetland zones exhibited high resistance to fire, and their present seral stage at the RNA for the most part is independent of seral stages in upland forest. No non-native species were present in the transects before or after the 1996 fire. Early establishment of new plants was limited to *Chamerion angustifolium* var. *canescens* and *Pinus contorta* var. *latifolia*. *Chamerion* was the only post-disturbance invader, present within one year in all communities except *Carex* fen and *Vaccinium*

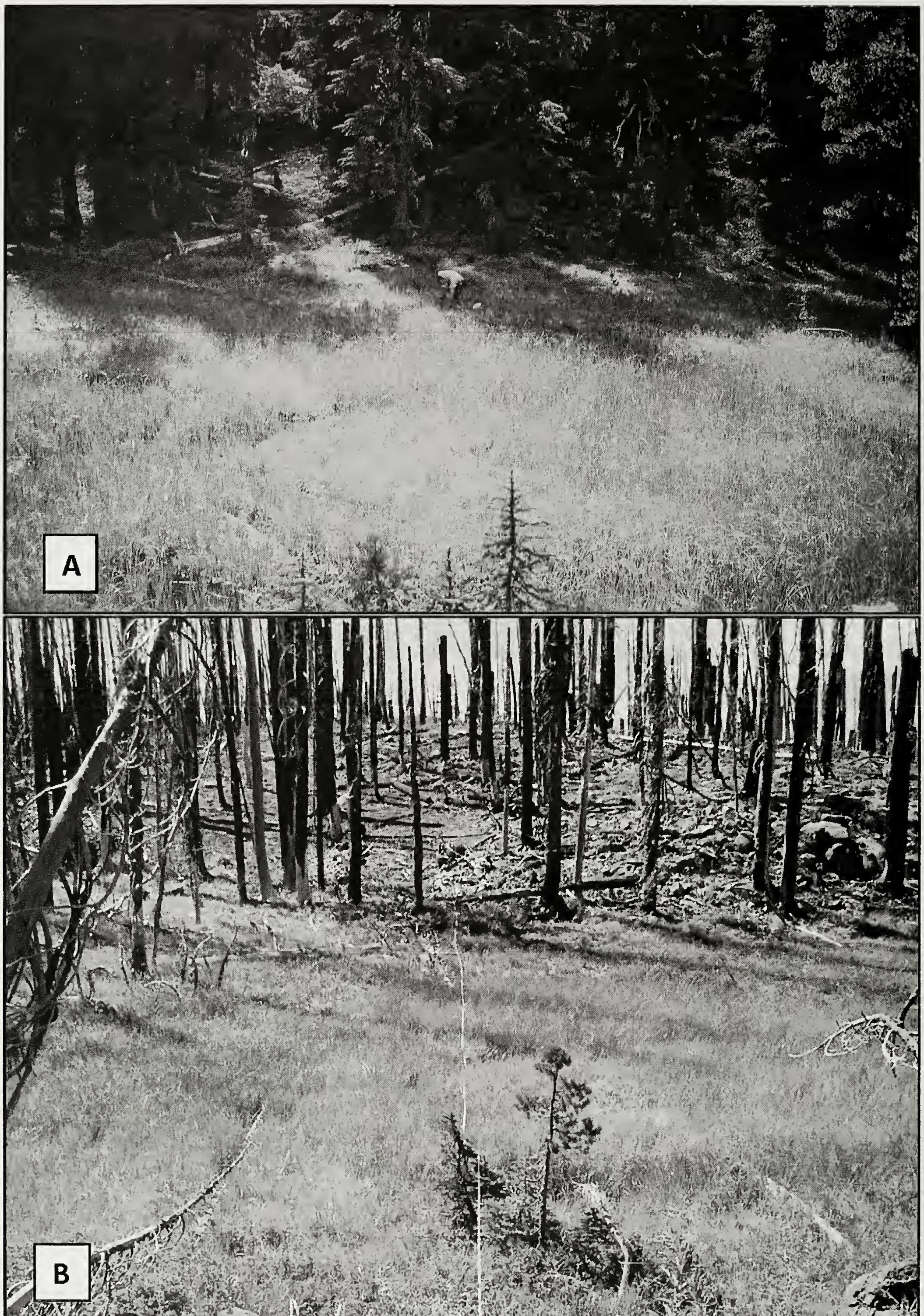

FIG. 10. Original 1976 transect, view to south. A. 1981, before fire. B. 2006, 10 years after fire. Transect length = 55 m.

FIG. 11. *Polytrichum commune* moss bed community. A. 1981, before fire. B. 2005, nine years after fire.

TABLE 5. FIRE EFFECTS ON PLANT SPECIES AT TORREY-CHARLTON RNA. Recovery times are minimal estimates from individual plots.

	Species	Fire effect
Vascular Plants	*Abies amabilis*	Complete kill
	Abies lasiocarpa	Complete kill
	Calamagrostis canadensis	Top kill or complete kill, slow to recover, increaser in wettest zones
	Chamerion angustifolium	Ephemeral increaser
	Deschampsia cespitosa	Top kill or complete kill, slow to recover
	Gaultheria humifusa	Top kill or complete kill, very slow to recover
	Kalmia microphylla	Top kill or complete kill, recovery 7 yr
	Lonicera caerulea	Top kill or complete kill, very slow to recover
	Picea engelmannii	Complete kill
	Pinus contorta var. *latifolia*	Complete kill, except on tree islands 16–24 m from burned perimeter
	Pinus monticola	Complete kill
	Rubus lasiococcus	Top kill, recovery 2 yr
	Spiraea splendens	Top kill or complete kill, very slow to recover
	Tsuga mertensiana	Complete kill, except on tree islands 16–24 m from perimeter
	Vaccinium deliciosum	Top kill or complete kill, recovery 7 yr
	Vaccinium membranaceum	Top kill or complete kill, recovery 2 yr
	Vaccinium scoparium	Top kill or complete kill, recovery 7 yr
	Vaccinium uliginosum	Top kill or complete kill, recovery 7 yr
	Xerophyllum tenax	Top kill or complete kill, recovery 9 yr
Bryophytes	*Ceratodon purpureus*	Increaser yr 3, ephemeral
	Marchantia polymorpha (s.l.)	Increaser yr 1–2, ephemeral
	Polytrichum commune	Top kill or complete kill, recovery 9 yr
	Polytrichum juniperinum	Increaser yr 7
	Sphagnum capillifolium	Top kill or complete kill, recovery 6 yr

uliginosum shrub swamp. Three years after the fire, it was most abundant in the *Xerophyllum tenax* ecotone, but with an average cover of only 3%. In contrast, post-fire densities in uplands at Yellowstone National Park reached 4.8 sprouts/m^2 two years after the fire and 23.4 sprouts/m^2 after five years (Turner et al. 1997). At Torrey-Charlton RNA, seed sources for *Chamerion* may have been limited, or post-fire surface conditions may not have been favorable for establishment. *Chamerion* was most consistently found in the *Xerophyllum tenax* ecotone, but its failure to expand may be due to environmental factors or competition, because most species there quickly recovered to near pre-burn abundance.

FIG. 12. Soil crust (*Ceratodon purpureus*, *Polytrichum juniperinum*) in 2005, nine years after fire. Scale intervals = 10 cm.

Around the margins of the wetlands at the RNA, survival of shrubs and herbs was limited to resprouting, extension of rhizomes, or other vegetative mechanisms from surviving plants. Increased light and nutrients available after the fire provided only limited advantage to surviving species, because of their restriction to moisture gradients. However, survival of *Vaccinium cespitosum, V. deliciosum, V. membranaceum, V. scoparium,* and *Rubus lasiococcus* indicates that these habitats may serve as important sources for dispersal and recolonization of uplands and other wetlands (Hill and Vander Kloet 2005). Recruitment of burned snags in the wetlands will provide substrate for establishment of new shrub swamp, sphagnum hummocks, and tree islands.

CONCLUSIONS

Because wetland soils at Torrey Lake Fen were hydrated at the time of the fire, wetland plant communities sustained relatively superficial damage compared to the catastrophic effect on upland *Tsuga mertensiana* forest. Fire damage was inversely proportional to moisture gradient, and recovery of both vascular plants and bryophytes more or less directly proportional to the gradient. Fire effects persisted 12 yr after the fire in the form of reduced total percent cover, and changes in the percent cover of component vegetative layers. Cover of shrub, forb, grass, and moss layers declined in vegetation zones at the drier end of the moisture gradient, but increased in grass and sedge-dominated zones at the wetter end of the gradient, at the expense of forb, grass, and sedge layers.

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LITERATURE CITED

ACKER, S. A., J. KERTIS, H. BRUNER, K. O'CONNELL, AND J. SEXTON. 2013. Dynamics of coarse woody debris following wildfire in a mountain hemlock (*Tsuga mertensiana*) forest. Forest Ecology and Management 302:231–239.

AGEE, J. K. AND L. SMITH. 1984. Subalpine tree reestablishment after fire in the Olympic Mountains, Washington. Ecology 65:810–819.

ATTIWILL, P. M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. Forest Ecology and Management 63:247–300.

BELKNAP, J., J. H. KALTENECKER, R. ROSENTRETER, J. WILLIAMS, S. LEONARD, AND D. ELDRIDGE. 2001. Biological soil crusts: ecology and management. United States Department of the Interior (USDI) Bureau of Land Management Technical Reference 1730-2, BLM/ID/ST-01/001+1730. United States Department of the Interior Bureau of Land Management Printed Materials Distribution Center, Denver, CO.

CHRISTY, J. A. 2001. Wetland vegetation of Fanno Meadows Preserve, Polk County, Oregon. Unpublished report to The Nature Conservancy. Oregon Natural Heritage Information Center, Portland, OR.

———. 2003. Summary of vegetation studies, 1980–2002, Gold Lake Bog Research Natural Area, Willamette National Forest, Lane County, Oregon. Unpublished report to United States Department of Agriculture Forest Service. Oregon Natural Heritage Information Center, Oregon State University Institute for Natural Resources, Corvallis, OR.

———. 2004. Native freshwater wetland plant associations of northwestern Oregon. Oregon Natural Heritage Information Center, Oregon State University Institute for Natural Resources, Corvallis, OR.

———. 2005a. Sphagnum fens on the Oregon coast: diminishing habitat and need for management. Unpublished report to United States Fish and Wildlife Service. Oregon Natural Heritage Information Center, Oregon State University Institute for Natural Resources, Corvallis, OR.

———. 2005b. Vegetation and stand history of Henderson Fen, Sycan Marsh Preserve, Lake County, Oregon. Unpublished report to The Nature Conservancy. Oregon Natural Heritage Information Center, Oregon State University Institute for Natural Resources, Corvallis, OR.

——— AND J. H. TITUS. 1998. Vegetation of Hidden Lake Fen, Blue River Ranger District, Willamette National Forest, Oregon. Unpublished report to USDA Forest Service, Oregon Natural Heritage Program, Portland, OR.

COOK, T., S. C. MEYERS, AND S. SUNDBERG (eds.). 2013. Oregon Vascular Plant Checklist. Version 1.3. Website http://oregonflora.org/checklist.php (accessed 29 August 2013).

CRAMER, J. R. 2005. The Biscuit Fire and the flora of serpentine fens: differences in species composition between burned and unburned fens. M.S. thesis. University of Vermont, Burlington, VT.

CREMER, W. AND A. B. MOUNT. 1965. Early stages of plant succession following the complete felling and burning of *Eucalyptus regnans* forest in the Florentine Valley, Tasmania. Australian Journal of Botany 13:303–322.

DEBENEDETTI, S. H. AND D. J. PARSONS. 1984. Postfire succession in a Sierran subalpine meadow. American Midland Naturalist 111:118–125.

DICKMAN, A. W. 1984. Fire and *Phellinus weirii* in a mountain hemlock (*Tsuga mertensiana*) forest: postfire succession and the persistence, distribution, and spread of a root-rotting fungus. PhD dissertation. University of Oregon, Eugene, OR.

——— AND S. COOK. 1989. Fire and fungus in a mountain hemlock stand. Canadian Journal of Botany 67:2005–2016.

FRENKEL, R. E., W. H. MOIR, AND J. A. CHRISTY. 1986. Vegetation of Torrey Lake Mire, central Cascade Range, Oregon. Madroño 33:24–39.

FRYER, J. L. 2008. *Polytrichum juniperinum*. *In* Fire Effects Information System (FEIS), [Online] United States Department of Agriculture Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, MT. Website http://www.fs.fed.us/database/feis/ (accessed 29 August 2013).

GARDNER, J. J. AND C. WHITLOCK. 2001. Charcoal accumulation following a recent fire in the Cascade Range, northwestern USA, and its relevance for fire-history studies. The Holocene 11:541–549.

GUERRANT, E. O., S. T. SCHULTZ, AND D. K. IMPER. 1998. Recovery plan for the endangered western lily (*Lilium occidentale*). U.S. Fish and Wildlife Service, Portland, OR.

HANSEN, H. P. 1941. Paleoecology of two peat deposits on the Oregon coast. Oregon State Monographs, Studies in Botany 3:1–31.

———. 1944. Further pollen studies of peat bogs on the Pacific coast of Oregon and Washington. Bulletin of the Torrey Botanical Club 71:627–636.

HEBDA, R. J., K. GUSTAVSON, K. GOLINSKI, AND A. M. CALDER. 2000. Burns Bog ecosystem review synthesis report for Burns Bog, Fraser River Delta, Southwestern British Columbia, Canada. Environmental Assessment Office, Victoria, BC.

HEINSELMAN, M. L. 1963. Forest sites, bog processes, and peatland types in the Glacial Lake Agassiz

Region, Minnesota. Ecological Monographs 33:327–374.

HILL, N. M. AND S. P. VANDER KLOET. 2005. Longevity of experimentally buried seed in *Vaccinium*: relationship to climate, reproductive factors and natural seed banks. Journal of Ecology 93: 1167–1176.

KUHRY, P. 1994. The role of fire in the development of *Sphagnum*-dominated peatlands in western boreal Canada. Journal of Ecology 82:899–910.

——— AND J. TURUNEN. 2006. The postglacial development of boreal and subarctic peatlands. Pp. 25–46 *in* R. K. Wieder and D. H. Vitt (eds.), Boreal Peatland Ecosystems. Ecological Studies 188:1–435.

KUNZE, L. M. 1994. Preliminary classification of native, low elevation, freshwater wetland vegetation in western Washington. Washington Natural Heritage Program, Department of Natural Resources, Olympia, WA.

MALTBY, E., C. J. LEGG, AND M. C. F. PROCTOR. 1990. The ecology of severe moorland fire on the North York Moors: effects of the 1976 fires, and subsequent surface and vegetation development. Journal of Ecology 78:490–518.

MARTIN, R. C. AND R. E. FRENKEL. 1978. Preserve analysis: Blacklock Point. Oregon Natural Area Preserves Advisory Committee. State Land Board, Salem, OR.

MATLACK, G. R., D. J. GIBSON, AND R. E. GOOD. 1993. Clonal propagation, local disturbance, and the structure of vegetation: ericaceous shrubs in the Pine Barrens of New Jersey. Biological Conservation 63:1–8.

MATTHEWS, R. F. 1993. *Marchantia polymorpha. In* Fire Effects Information System (FEIS), [Online] United States Department of Agriculture Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, MT. Website http://www.fs.fed.us/database/feis/ (accessed 29 August 2013).

MCCAIN, C. AND N. DIAZ. 2002. Field guide to the forested plant associations of the westside central Cascades of northwest Oregon; Willamette N.F., USFS; Mt. Hood N.F., USFS; Salem District, BLM; Eugene District, BLM. USDA Forest Service Technical Paper R6-NR-ECOL-TP-02-02.

MOORE, P. D. AND D. J. BELLAMY. 1974. Peatlands. Springer-Verlag, New York, NY.

MURRAY, M. 2000. Wetland plant associations of the western hemlock zone in the central coastal and Cascade Mountains. Oregon Natural Heritage Program, Portland, OR.

PONZETTI, J. M., B. MCCUNE, AND D. A. PYKE. 2007. Biotic soil crusts in relation to topography, cheatgrass and fire in the Columbia Basin, Washington. The Bryologist 110:706–722.

PYNE, S. J., P. L. ANDREWS, AND R. D. LAVEN. 1996. Introduction to wildland fire. 2nd ed. John Wiley and Sons, Inc, New York, NY.

RATCHFORD, J. S., S. E. WITTMAN, E. S. JULES, A. M. ELLISON, J. J. GOTELLI, AND N. J. SAUNDERS. 2005. The effects of fire, local environment and time on ant assemblages in fens and forests. Diversity and Distributions 11:487–497.

ROWE, J. S. AND G. W. SCOTTER. 1973. Fire in the boreal forest. Quaternary Research 3:444–464.

SALIX ASSOCIATES. 1998. Establishment record for Torrey-Charlton Research Natural Area within Willamette and Deschutes National Forests, Lane and Deschutes Counties, Oregon. Unpublished report to USDA Forest Service, Eugene, OR.

SANDERS, N. J., N. J. GOTELLI, S. E. WITTMAN, J. S. RATCHFORD, A. M. ELLISON, AND E. S. JULES. 2007. Assembly rules of ground-foraging ant assemblages are contingent on disturbance, habitat and spatial scale. Journal of Biogeography 34: 1632–1641.

SCHULTZ, S. T. 1989. Status report on *Lilium occidentale* Purdy. Unpublished report to Endangered Species Program, Oregon State Department of Agriculture. University of British Columbia, Vancouver.

SEYER, S. C. 1979. Vegetative ecology of a montane mire, Crater Lake National Park, Oregon. M.S. thesis. Oregon State University, Corvallis, OR.

———. 1981. Survey of vegetation of 18 lakes in Wallowa-Whitman National Forest, Oregon. Unpublished report to USDA Forest Service Forest Science Laboratory, Corvallis, OR.

———. 1983. Ecological analysis, Multorpor Fen Preserve, Oregon. Unpublished report to The Nature Conservancy, Oregon Field Office, Portland, OR.

TALLIS, J. H. 1983. Changes in wetland communities. Pp. 311–347 *in* A. J. P. Gore (ed.), Mires: swamp, bog, fen and moor, Ecosystems of the World, Vol. 4.

TESKY, J. L. 1992. *Ceratodon purpureus. In* Fire Effects Information System (FEIS), [Online] United States Department of Agriculture Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, MT. Website http://www.fs.fed.us/database/feis/ (accessed 29 August 2013).

THOMAS, P. A., M. C. F. PROCTOR, AND E. MALTBY. 1994. The ecology of severe moorland fire on the North York Moors: chemical and pH constraints on moss establishment from spores. Journal of Ecology 82:457–474.

TIEDEMANN, A. R., C. E. CONRAD, J. H. DIETERICH, J. W. HORNBECK, W. F. MEGAHAN, L. A. VIERECK, AND D. D. WADE. 1979. Effects of fire on water, a state-of-knowledge review. United States Department of Agriculture Forest Service General Technical Report WO-10.

TITUS, J. H. AND J. A. CHRISTY. 1997. Vegetation of Big Marsh, Deschutes National Forest, Oregon. Unpublished report to Deschutes National Forest. Oregon Natural Heritage Program, Portland, OR.

TOLMAN, D. A. 2006. Characterization of the ecotone between Jeffrey pine savannas and *Darlingtonia* fens in southwestern Oregon. Madroño 53:199–210.

———. 2007. Soil patterns in three *Darlingtonia* fens of southwestern Oregon. Natural Areas Journal 27:374–384.

TORGERSON, E. F., J. MCWILLIAMS, AND C. J. MCMURPHY. 1949. Soil survey, Astoria area, Oregon. United States Department of Agriculture Bureau of Plant Industry, Soils, and Agricultural Engineering. Series 1938, Number 20:1–80.

TURNER, M. G., W. H. ROMME, R. H. GARDNER, AND W. W. HARGROVE. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs 67: 411–433.

Western Regional Climate Center. 2010. Monthly total precipitation (inches) for Oakridge Fish Hatchery, Oregon, 1914–2010. Website http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?or6213 (accessed 15 December 2010).

Wilson, C. E. 1986. Floristic and edaphic aspects of vegetational patterns in subalpine mires of the Cascade Mountains of Oregon. M.S. thesis. University of Oregon, Eugene, OR.

Zobel, D. B. and J. A. Antos. 1997. A decade of recovery of understory vegetation buried by volcanic tephra from Mount St. Helens. Ecological Monographs 67:317–344.